

SEXUAL SIZE DIMORPHISM OF THE MUSK DUCK

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ABSTRACT.—We examined sexual size dimorphism of a lek-displaying diving duck from Australia, the Musk Duck (*Biziura lobata*). Like other lek-displaying species, Musk Ducks exhibit extreme sexual size dimorphism in addition to structural dimorphism. Body mass ratios (male:female) for Musk Ducks are among the highest reported for birds (more than 3:1). Multivariate analyses of 16 anatomical measurements indicated that body plans of male and female Musk Ducks have diverged isometrically except for the addition of a pendant lobe on lower mandibles of males. Within males, pendant lobe length, depth, and breadth were positively correlated with center rectrix length and bill width. Lobe area also was positively related to bill width, but not to center rectrix length. Lobe breadth and center rectrix length were positively related to overall body mass. Our results suggested that information about male physical quality may be conveyed to other Musk Ducks by parts of the anatomy most conspicuously exposed during sexual advertising displays. In contrast, anatomical features that function in foraging activity showed no sexual differences in anatomical shape relative to other parts of the anatomy that do not serve obvious foraging functions. We argue that foraging niche divergence or use of different food resources, if they have occurred, probably are secondary consequences of sexual size dimorphism. Received 28 March 2000, accepted 18 August 2000.

The Musk Duck (*Biziura lobata*) is a lek-displaying diving duck endemic to deep water wetlands, river systems, and coastal oceanic waters of temperate Australia (Frith 1967, Marchant and Higgins 1990, Johnsgard and Carbonell 1996). As an undivided basal lineage distant from other waterfowl, Musk Ducks show marked morphological and ecological convergence with *Nomonyx-Oxyura* stiff-tail ducks and deep-water divers such as eiders (*Somateria*, *Polysticta*) and steamer ducks (*Tachyeres*; McCracken et al. 1999; but see Livezey 1986, 1995). Musk Ducks also show extreme sexual size dimorphism.

The heaviest male Musk Duck reportedly weighed 3870 g (Serventy and Whittell 1962), whereas the smallest female weighed 993 g (Frith 1967), more than a three-fold difference in overall body mass. The average size dimorphism ratio (male:female) reported by Frith (1967) for a sample of 535 Musk Ducks was 1.55:1 (max. = 3.14) and ranks sixth among 47 lek-breeding bird species surveyed by Oakes (1992). With the exception of a few

other promiscuous anatids (*Asarcornis scutulata*, mean = 1.45, max. = 2.00; *Cairina moschata*, mean = 1.44, max. = 3.64) and two flightless species (*Tachyeres pternes*, mean = 1.43, max. = 1.70; *Anas aucklandica*, mean = 1.43, max. = not available), most waterfowl show average sexual body mass dimorphism ratios well below 1.4:1 (Johnsgard 1978, Madge and Burn 1988, Marchant and Higgins 1990, Dunning 1993).

Observational data (Frith 1967, Marchant and Higgins 1990, McCracken 1999) suggest that male emancipation from parental care and evolution of a lek mating system led to fixation of larger body size and other secondary sexual characters in male Musk Ducks (Fisher 1930, Møller 1990, Zuk et al. 1990). An alternative hypothesis not related to mating system theory is that niche divergence, perhaps driven by intersexual competition for food resources, is responsible for observed patterns of size dimorphism in Musk Ducks (Selander 1972, Nudds and Kaminski 1984, Slatkin 1984). Male and female Musk Ducks differ so greatly in size that the sexes probably occupy different foraging niches; however, little information about diets of this species currently is available (see Gamble 1966). We believe that insight into the forces responsible for Musk Duck sexual size dimorphism can be gained by measuring and comparing size and shape characteristics between sexes (Alisauskas 1987, Webster 1997). If aspects of the mating system primarily are responsible for

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sexual size dimorphism, we predicted that non-isometric patterns of dimorphism would be correlated with secondary sexual features associated with particular advertising displays. For Musk Ducks, the size and shape of the pendant lobe that hangs below the lower mandible or the length of the tail feathers are obvious possibilities because these parts of the anatomy are used almost exclusively in sexual displays (Johnsgard 1966, Frith 1967, Marchant and Higgins 1990, McCracken 1999). If niche divergence has occurred, we predicted that stronger patterns of sexual dimorphism would be evident in the feeding apparatus or other associated anatomical features that would allow one sex to gain access to different food resources than the other.

We tested the null hypothesis that male and female Musk Ducks show no differences in anatomical shape, independent of general body size. We also analyzed patterns of variation among males to evaluate the relative contribution of different body parts towards total size variation and determined whether the size of body parts were correlated with one another. We paid particular attention to anatomical features (e.g., lobe size and shape, tail length, tarsus length, etc.) hypothesized to have evolved for different functions such as sexual display, foraging, and locomotion. Lastly, we examined whether individuals differed in size or shape by capture method. Our measurements are the first for males and females captured at the same locality in more than 30 years and include many features of the anatomy previously not recorded (Frith 1967, Braithwaite and Frith 1969, Briggs 1988).

STUDY AREA AND METHODS

We captured, measured, banded, and released 46 Musk Ducks (29 males, 17 females) at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia (35° 55' S, 137° 25' E) between 11 September 1995 and 19 October 1997. We used three capture methods: night-lighting (31 captures; Bishop and Barratt 1969), baited clover-leaf traps (12 captures; Addy 1956), and walk-in-nest-traps (3 captures; Dietz et al. 1994).

Morphometrics.—We recorded 12 measurements for each captured duck: bill length (± 0.1 mm), bill width (± 0.1 mm), bill height (± 0.1 mm), head length (± 1 mm), tarsus length (± 0.1 mm), tarsus bone length (± 0.1 mm), total length (± 5 mm), wing span (± 5 mm), wing chord (± 1 mm), 9th primary length (± 1

mm), center rectrix length (± 0.1 mm), and body mass (± 50 g). We also measured (± 0.1 mm) length, depth, and breadth of lobes on males (females possess only small vestigial lobes; six were measured). Lobes for all but two males (too small to trace) were traced in the field. Lobe outlines subsequently were transferred to dry paper, cut out, and weighed (± 0.01 g), whereby the total area (cm^2) of the lobe was calculated by dividing the mass of each lobe outline by the density (g/cm^2) of the paper. We recorded age (hatching year/after hatching year) as indicated by the presence or absence of natal down notches on tail feathers (Bellrose 1980). Wing and tail molts also were recorded.

Statistical analyses.—We used multivariate analysis of covariance (MANCOVA) to test whether morphometric measurements (excluding those describing the sub-mandibular lobe) differed between sexes and capture methods or varied with capture date (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996). Capture methods included in the model were night-lighting and baited clover-leaf traps; three females captured on the nest were omitted from the analysis. We began with a saturated model containing sex and capture method as explanatory variables, capture date as a covariate, and all possible interactions. Nonsignificant interactions and covariates were removed iteratively, starting with the highest order interactions, and the analysis was repeated until a single most parsimonious model containing only sex and capture method was obtained. *F*-values reported from multivariate analysis of variance (MANOVA) were determined using Wilks' λ . Following a significant MANOVA, we used analysis of variance (ANOVA) to test whether individual body measurements differed between sexes and capture methods. We report least squares means and standard errors (\pm SE) for morphometric variables that differed between capture methods (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996); unadjusted means and standard deviations (\pm SD) are given in Table 1. In light of significant sexual differences in all measurements ($P < 0.001$), we used the CANONICAL option in the MANOVA statement (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) to examine the canonical axes that best distinguish the sexes morphologically and determine the relative contribution of each dependent variable to sex separation (see Hatcher and Stepanski 1994). We used a *G*-test to determine if sex ratios differed between capture methods.

To test the null hypothesis that males and females show no differences in anatomical shape, independent of overall body size, we performed principal components analysis (PCA; PROC PRINCOMP; SAS 6.12; SAS Institute, Inc. 1996) using the correlation matrix of the same 12 metric variables to construct one index of overall body size (PC1) and eleven indices of shape (PC2–12). Corresponding principal component scores for each individual were subsequently entered into a MANOVA (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) to create a single linear model, including sex and capture method as explanatory variables and the 12 principal component scores as response vari-

TABLE 1. Body size measurements (mm or cm²) and body mass (g) for male and female Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Male			Female			<i>P</i> ^a	CAN1 ^b
	<i>n</i>	Mean ± SD	Range	<i>n</i>	Mean ± SD	Range		
Bill length	29	40.19 ± 1.00	37.3–42.1	17	35.01 ± 1.23	32.7–37.0	0.001	1.32
Bill width	29	36.30 ± 1.21	34.1–39.1	17	30.15 ± 2.37	28.0–37.6	0.001	0.54
Bill depth	29	34.97 ± 2.26	32.3–43.5	17	28.64 ± 1.09	26.4–30.4	0.001	0.81
Head length	29	103.4 ± 3.0	97–111	17	90.6 ± 3.1	84–95	0.001	0.39
Lobe length	29	71.17 ± 18.18	37.7–102.4	6	33.13 ± 1.80	31.0–36.0	—	—
Lobe depth	29	62.42 ± 21.48	11.6–99.5	6	6.87 ± 1.22	5.0–8.0	—	—
Lobe breadth	29	31.93 ± 4.00	21.7–39.7	6	20.22 ± 0.84	18.7–21.1	—	—
Lobe area	27	37.60 ± 18.32	8.1–69.1	—	—	—	—	—
Tarsus length	29	63.05 ± 2.90	57.7–69.8	17	53.66 ± 2.88	49.1–60.4	0.001	−0.59
Tarsus bone length	29	51.43 ± 2.49	44.5–56.0	17	44.00 ± 2.36	41.0–50.4	0.001	−0.08
Total length	27	664.6 ± 23.6	610–710	15	552.7 ± 17.3	530–580	0.001	0.92
Wing span	26	874.5 ± 41.5	770–960	13	723.8 ± 26.9	650–760	0.001	0.65
Wing chord	26	226.3 ± 8.6	205–240	13	183.7 ± 4.7	175–190	0.001	1.17
9th primary	26	164.6 ± 19.2	130–210	13	126.8 ± 12.2	102–140	0.001	0.36
Center rectrix	27	117.1 ± 9.0	91–130	12	96.2 ± 9.4	75–110	0.001	−0.12
Body mass	29	2560.2 ± 331.3	1700–3100	17	1560.9 ± 245.3	1150–1910	0.001	−0.41

^a ANOVAs for sex effect were adjusted for capture method (1, 33 df for each test; lobe measurements excluded). Measurements shown in the table were not adjusted for capture method. Molting soft parts not fully grown were omitted from the tests.

^b Standardized between sex canonical coefficients were adjusted for capture method.

ables (see also Alisauskas 1998). Following a significant MANOVA, we used ANOVA to test whether individual principal components describing size (PC1) and shape (PC2–12) differed between sexes and capture methods.

To analyze anatomical patterns of variation among males, we performed a second principal components analysis and MANOVA (PROC GLM; SAS 6.12; SAS Institute, Inc. 1996) using the same 12 measurements plus the 4 lobe measurements and capture method as the independent variable. We regressed the 4 lobe measurements on each of the other 12 measurements using analysis of covariance (ANCOVA; PROC GLM, SAS 6.12; SAS Institute, Inc. 1996) to determine if lobe

dimensions were correlated with size of other anatomical features and whether these relationships differed between Musk Ducks caught by night-lighting or baited clover-leaf traps. Center rectrix length was regressed on all non-lobe measurements using ANCOVA. For both sets of analyses, total length was adjusted for the length of the tail by subtracting the length of the center rectrix.

RESULTS

Variation between sexes and capture methods.—All Musk Ducks measured in our study were after-hatching year birds. Overall body size differed between sexes (MANOVA: $F = 37.51$, 12, 22 df, $P < 0.001$) and capture methods (MANOVA: $F = 3.05$, 12, 22 df, $P = 0.011$). Overall body size did not vary with capture date, and no interaction was significant (all P s > 0.05). All measurements were significantly larger for males than for females (Table 1, Fig. 1). Measurements contributing the most to sex separation, in order of decreasing contribution included bill length, wing chord, total length, and bill depth (CAN1; Table 1). Wing span and head length showed no overlap in absolute size (Table 1). Measurements contributing the least to sex separation included tarsus bone length and center rectrix length. Three of 12 measurements differed significantly between capture methods (all

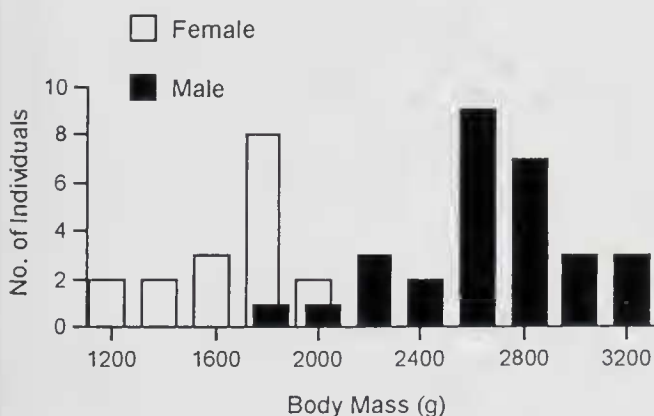


FIG. 1. Frequency distribution of body mass for adult male ($n = 29$) and female ($n = 17$) Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

TABLE 2. Eigenvectors for principal components analysis of pooled anatomical measurements for male and female Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Eigenvectors		
	PC1	PC2	PC3
Total length	0.3140	0.1012	0.0279
Wing chord	0.3093	0.0028	0.0823
Bill width	0.3049	0.0475	-0.1889
Bill length	0.3020	-0.1013	-0.1641
Wing span	0.3003	-0.0647	0.2228
Head length	0.2942	-0.1672	-0.2306
Body mass	0.2912	0.0754	-0.3679
Tarsus length	0.2905	-0.2934	0.4080
Tarsus bone length	0.2791	-0.3501	0.4609
Bill depth	0.2704	-0.2666	-0.4971
Ctr. rectrix length	0.2584	0.5314	0.2560
9th primary	0.2407	0.6142	0.0088

other $P_s > 0.05$). Musk Ducks caught by night-lighting had longer tarsi than those caught in baited clover-leaf traps (night-lighting least squares mean \pm SE = 58.64 \pm 0.58 mm, clover-leaf traps = 56.39 \pm 0.86 mm; ANOVA: $F = 5.26$, 1, 33 df, $P = 0.028$). Ninth primary (night-lighting = 139.6 \pm 3.2 mm, clover-leaf traps = 161.5 \pm 4.7 mm; ANOVA: $F = 16.85$, 1, 33 df, $P < 0.001$) and center rectrix (night-lighting = 105.1 \pm 1.9 mm, clover-leaf traps = 111.9 \pm 2.8 mm; ANOVA: $F = 4.44$, 1, 33 df, $P = 0.043$) showed the opposite relationship. Sex ratios also differed by capture method ($G = 3.446$, 1 df, $P < 0.05$). Of 29 Musk Ducks captured by night-lighting 17 were male and 12 were female (male:female = 1.42:1), whereas 12 males and 2 females were captured in baited clover-leaf traps (male:female = 6.0:1).

Principal components analysis revealed three discernable patterns of variation in pooled male and female Musk Duck anatomical data, excluding lobe measurements. The first principal component (PC1) accounted for 79.2% of observed variation (eigenvalue = 9.51) and related to overall body size, as indicated by positive eigenvectors of approximately equal magnitude for all 12 measurements (Table 2). The second component (PC2) accounted for 6.7% of observed morphometric variation (eigenvalue = 0.80) and corresponded to a decrease in the size of the tarsus relative to the lengths of the 9th primary and

center rectrix (Table 2). The third component (PC3) accounted for an additional 3.7% of observed variation (eigenvalue = 0.45) and corresponded to a reduction in the size of the head and overall body mass relative to the size of the tarsus (Table 2). Informative anatomical trends were not evident in PC4–12 (eigenvalues ≤ 0.31). MANOVA indicated that one or more principal components differed significantly between sexes ($F = 37.51$, 12, 22 df, $P < 0.001$) and capture methods ($F = 3.05$, 12, 22 df, $P = 0.011$). Subsequent ANOVAs indicated that differences between sexes were limited to PC1 ($F = 422.04$, 1, 33 df, $P < 0.001$), and differences between capture methods were limited to PC2 ($F = 18.56$, 1, 33 df, $P < 0.001$); PC3–12 did not differ significantly between sexes or capture methods (PC3–12, all $P_s > 0.05$). Thus, excluding lobe characteristics and a component of morphometric variation related to capture bias (PC2), sexual divergence in Musk Duck morphology was isometric.

Variation among males.—Principal components analysis revealed three patterns of variation among males that may be of biological significance. The first 5 principal components (PC1–5) accounted for 75.2% of the observed morphometric variation and had corresponding eigenvalues of 1.13 or greater. Measurements most highly correlated with PC1 (26.9% of the total variation) were the 4 lobe measurements (Table 3). The next most highly correlated measurements were bill width, body mass, and center rectrix length. Other measurements expected to be associated with flight and diving proficiency (e.g., wingspan, wing chord, 9th primary, tarsus length, tarsus bone) were not highly correlated (PC1 eigenvectors absolute magnitudes ≤ 0.105). Male variation in these measurements instead appeared to be evident in PC2 (19.3% of the total variation), in which tarsus length, tarsus bone length, wingspan, and wing chord measures showed larger correlations than other measurements (Table 3). The third principal component (PC3) made up an additional 11.6% of the total variation in males and differed between capture methods (ANOVA: $F = 24.57$, 1, 22 df, $P < 0.001$). Lucid anatomical trends were not readily evident in any other principal components, and no other com-

TABLE 3. Eigenvectors for principal components analysis of anatomical measurements for male Musk Ducks at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995–1997.

Measurement	Eigenvectors				
	PC1	PC2	PC3	PC4	PC5
Lobe area	0.4481	-0.1173	-0.0281	-0.0963	0.0989
Lobe length	0.4431	-0.0544	-0.1412	-0.1526	0.0836
Lobe depth	0.4238	-0.0029	-0.2152	-0.0926	0.0779
Lobe breadth	0.4154	-0.0842	0.0062	0.0276	-0.0285
Bill width	0.2377	0.1885	-0.1369	0.4121	-0.3130
Body mass	0.2282	0.1052	0.4375	0.1580	-0.2197
Ctr. rectrix length	0.1792	0.1720	0.3263	-0.4371	-0.0229
Total length	0.1743	0.2596	0.4465	0.0864	-0.0180
Bill length	0.1689	0.0355	0.0808	0.3086	0.4529
Bill depth	0.1450	0.2606	-0.1546	0.2002	-0.4078
Wing span	-0.1047	0.4444	0.1082	-0.0360	-0.0533
Tarsus bone length	-0.0974	0.4448	-0.1767	-0.1058	0.1572
Wing chord	0.0751	0.3330	-0.1162	-0.3161	0.4166
9th primary	-0.0580	-0.0357	0.5535	0.0030	0.1357
Tarsus length	-0.0257	0.5059	-0.1519	0.0947	0.0321
Head length	-0.0020	-0.0031	0.0255	0.5551	0.4871

ponents differed between capture methods (ANOVAs: all $P_s > 0.05$).

The length, depth, and breadth of the lobe were positively related to center rectrix length and bill width (Figs. 2A, 3). Lobe area also was positively related to bill width (Fig. 3) but not to center rectrix length, and lobe breadth was positively related to overall body mass (Fig. 2B). No other linear relationships between lobe dimensions and other body parts were evident (all $P_s > 0.05$). Length of the center rectrix, which varied positively with lobe length, depth, and breadth (all $P_s \leq 0.028$; Fig. 2A), was positively related to body mass (Fig. 2B). Length of the center rectrix also varied positively with wing chord in males caught by night-lighting, but not in males caught in baited clover-leaf traps (Fig. 2B). Center rectrix length showed no significant linear relationship to bill width or any other non-lobe measurement (all $P_s > 0.05$), and no other measurements showed a capture effect (all $P_s > 0.05$).

DISCUSSION

Many authors have argued for a causal relationship between sexual size dimorphism and evolution of promiscuous mating behavior (e.g., Darwin 1871, Lack 1968, Payne 1984, Oakes 1992; but see Höglund 1989, Höglund and Sillén-Tullberg 1994). We found that 86% of male and female Musk Ducks

showed no overlap in body mass (Table 1, Fig. 1). This level of dimorphism ranks high in comparison with other dimorphic species and is among the highest ever recorded for lek-breeding birds. One possible explanation for the appearance of extreme sexual size dimorphism is that factors related to lek breeding (strong female selection for high quality males or competition among males for limited access to females) led to fixation of larger body size and other secondary sexual characters in male Musk Ducks. An alternative hypothesis, not related to the mating system, is that sexual competition for food resources (foraging niche divergence) led to sexual size dimorphism.

Sexual selection.—Our data indicated that the size of the lobe, width of the bill, body mass, and length of the center rectrix were significant elements of structural variation within male Musk Ducks (Table 3, Fig. 1). Among these, the length, depth, and breadth of the lobe increased linearly with the length of the center rectrix (Fig. 2A). It is not surprising that the lobe and tail feathers showed a significant correlation in this species, because these are the two features of the male anatomy that are prominently displayed during bouts of sexual display activity (Johnsgard 1966, Frith 1967, Marchant and Higgins 1990, McCracken 1999). In the paddle-plonk-whistle-kick display described by Johnsgard (1966) and others, the lobe swells with blood

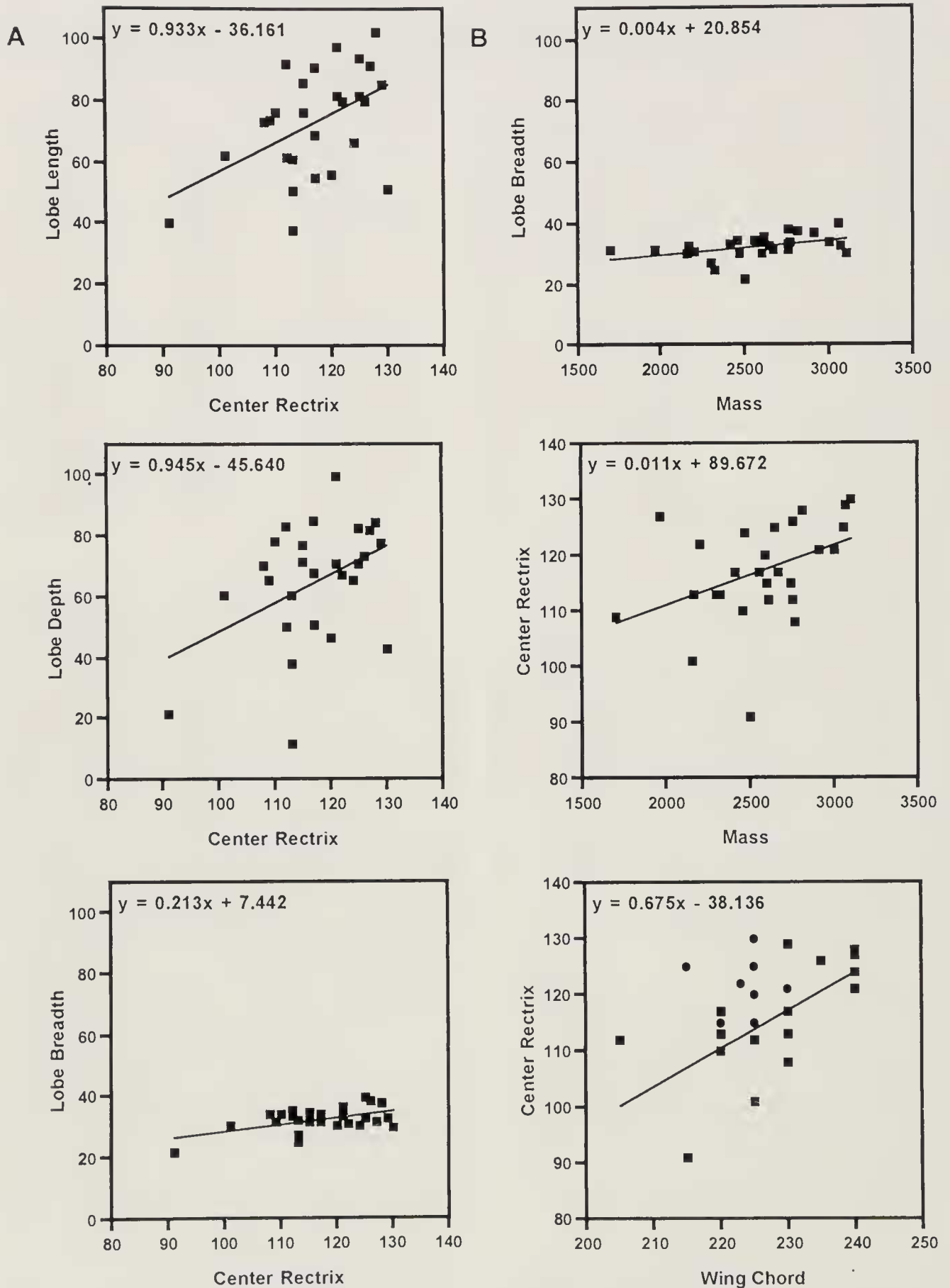


FIG. 2 (A) Relations between center rectrix length and lobe length ($F = 7.50$, 1, 25 df, $P = 0.011$, $R^2 = 0.23$), lobe depth ($F = 5.48$, 1, 25 df, $P = 0.027$, $R^2 = 0.18$), and lobe breadth ($F = 8.20$, 1, 25 df, $P = 0.008$, $R^2 = 0.25$) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997. (B) Relations between body mass and lobe breadth ($F = 4.62$, 1, 27 df, $P = 0.041$, $R^2 = 0.15$), body mass and center rectrix length ($F = 5.02$, 1, 25 df, $P = 0.034$, $R^2 = 0.17$), and wing chord length and center rectrix length (males captured by night-lighting indicated by squares, $F =$

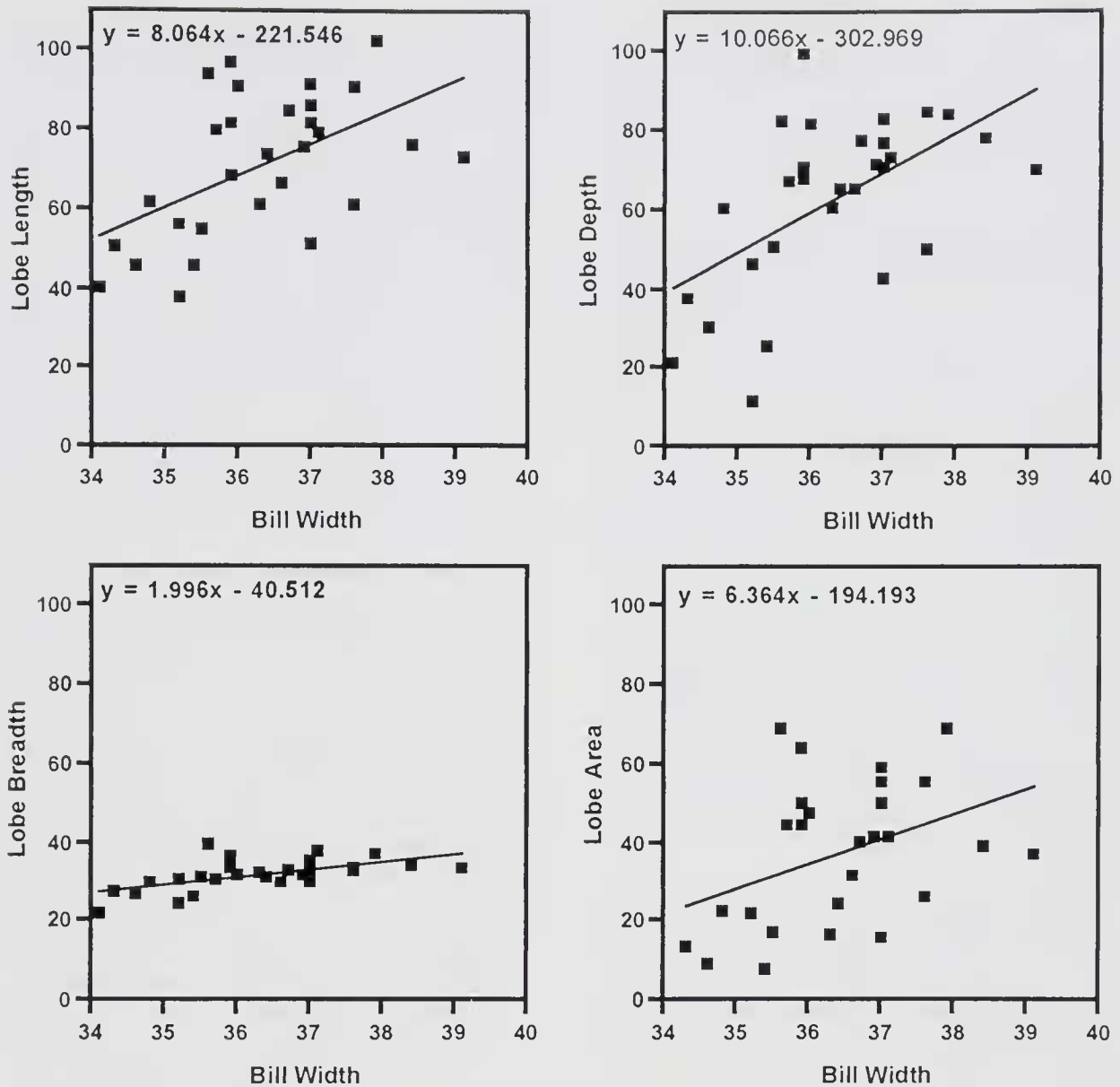


FIG. 3 Relations between bill width and lobe length ($F = 10.81$, 1, 27 df, $P = 0.0028$, $R^2 = 0.29$), lobe depth ($F = 12.64$, 1, 27 df, $P = 0.0014$, $R^2 = 0.32$), lobe breadth ($F = 15.34$, 1, 27 df, $P < 0.001$, $R^2 = 0.36$), and lobe area ($F = 4.72$, 1, 25 df, $P = 0.04$, $R^2 = 0.16$) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997.

and is thrust forward rhythmically to accompany coordinated splashing displays and vocalizations. At the same time, the tail is spread wide, repeatedly lifted, dropped to the surface of the water, and cocked over the back. Together, the swollen lobe and spread tail feathers create an unusual spectacle, but what do the lobe and tail feathers signal to other Musk Ducks?

Our data indicated that the size of the lobe is a true indicator of the width across the bill (Fig. 3). Other measurements, including bill length, bill depth, head length, various measures of the wings and tarsi, and adjusted total body length showed no relationships to lobe size. Width of the bill undoubtedly parallels the internal width of the gape and probably is a good estimate of a Musk Duck's ability to

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10.76, 1, 14 df, $P = 0.006$, $R^2 = 0.43$; males captured by baited clover-leaf traps indicated by circles, $F = 0.27$, 1, 8 df, $P = 0.05$, $R^2 = 0.03$, no regression line) of adult male Musk Ducks captured at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 1995-1997.

swallow large food items. The width of the bill also might factor importantly in fights with other males, the ability to seize females for copulation, and the capacity to out-compete other waterfowl for food by inflicting strong bites (see McCracken 1999). A wider gape might reflect the need for a stronger point of attachment of the lower mandible for Musk Ducks with larger lobes, and if larger lobes are more costly than smaller lobes, males that wear larger lobes may exhibit greater fitness (Zahavi 1975, 1977). Although the length of the center rectrix covaried with the dimensions of the lobe, unlike the lobe, it was not positively correlated with bill width. Center rectrix length instead was positively correlated with overall body mass, as was lobe breadth. These observations suggest that additional information about overall body size is presented in the parts of the anatomy most conspicuously exposed during sexual displays. In principle, there are many reasons why females might select males with wider gapes and greater body mass if both traits are advantageous and result in increased fitness to the parents and offspring.

To what extent the size of the lobe, length of the tail, and other anatomical features correlate with age or physical condition is unknown, because no information about growth rates, nutrient allocation, or parasite loads is available for Musk Ducks. If Musk Ducks continue to grow asymptotically beyond their first year of life (and this is very plausible), continued growth and sexual development could contribute to age-related differences in size and social dominance (see Alisauskas 1987). In particular, the size of the lobe and other measurements might be determined by growth during immature stages, with birds that are doing the poorest having proportionately smaller measurements (Møller 1990). Our identification of a capture bias may be evidence of such age-related growth patterns. Perhaps individuals captured by active means (i.e., night-lighting) were younger birds and more prone to capture because of their morphology or physical condition. Sex ratios also showed a capture bias. More than 4 times as many males per female were caught by baited clover-leaf traps than by night-lighting. One explanation for the different sex ratios in the two catches might be that males are socially

dominant to females (see also McCracken 1999). Males also may be more active than females and range over greater distances. In either case, documentation of the effects of age and physical condition on morphology and its relationship to social and reproductive status will require that marked Musk Ducks of known age be measured repeatedly over a period of several years. Such a study also could determine whether the size of the lobe can change with time depending on current physical condition or reproductive status.

Other factors that could have influenced sexual size dimorphism include limited and unpredictable access to females and potentially asynchronous female ovulation cycles as a result of an extended breeding season (McCracken et al. 2000). Data supporting this conclusion include classic lek behavior, an excess of male attendants at display bouts, male-biased sex ratios greater than 20:1 in some localities, and patterns of intra-specific aggression (McCracken 1999). Aggression may be reinforced by well-developed mandibular musculature and an unusually sharp nail on the bill. These observations are consistent with the idea that a combination of male and female mediated selective mechanisms have resulted in competitively successful males achieving greater access to receptive females.

Foraging niche divergence.—An alternative explanation of sexual foraging niche divergence as a cause of sexual size dimorphism (Selander 1972, Nudds and Kaminski 1984, Slatkin 1984) is not directly supported by our data. If the niche divergence hypothesis is correct, stronger patterns of sexual dimorphism than we observed should be evident in feeding apparatus and other associated anatomical features (i.e., the shape of the bill and the hindlimbs if underwater swimming efficiency is an important factor in foraging activity). However, we found that male Musk Ducks simply were isometrically larger than females with the addition of a pendant lobe and a longer tail that covaried with the lobe.

The absence of measurable differences in the shape of feeding apparatus, however, can not unequivocally exclude foraging niche divergence as a cause of sexual size dimorphism. Male and female Musk Ducks differ in overall body size by a factor of two to three; thus, size alone should influence rates and

modes of nutrient acquisition (Nudds and Kaminski 1984, Nudds and Bowlby 1984). Indeed, male and female Musk Ducks probably occupy different foraging niches. On Kangaroo Island, males occurred more often in near-shore marine environments than did females (McCracken 1999), and with mandibles averaging 14.8–22.1% larger than those of females for any given measurement (bill depth being the greatest), male Musk Ducks probably are capable of capturing and crushing larger, harder shelled prey. At Barrenbox Swamp, New South Wales, twice as many adult males (60%) consumed hard-shelled prey items such as freshwater mollusks as did females (30%; Gamble 1966). Such a relationship, if it is widespread, may confound efforts to distinguish cause from effect in this species.

To understand these patterns more completely, future studies of Musk Ducks will require some paternity work including a heritability analysis of male secondary sexual features, such the size of the lobe, length of the tail, and overall body mass. A study of foraging behavior focusing on prey and habitat selection (e.g., Goudie and Ankney 1988, Hamilton et al. 1999) also would be useful, as would comparisons with ecologically convergent, large-bodied divers such as eiders (*Somateria*, *Polysticta*) and steamer ducks (*Tachyeres*).

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